

EFFECTS OF SOIL OXIDATION-REDUCTION CONDITIONS ON INTERNAL OXYGEN TRANSPORT, ROOT AERATION, AND GROWTH OF WETLAND PLANTS

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Abstract—Characterization of hydric soils and the relationship between soil oxidation-reduction processes and wetland plant distribution are critical to the identification and delineation of wetlands and to our understanding of soil processes and plant functioning in wetland ecosystems. However, the information on the relationship between flood response of wetland plants and reducing soil conditions is limited. We have examined the influence of intensity and capacity of soil reduction on internal oxygen transport, rhizosphere oxygenation, nutrient uptake, root and shoot growth, and survival of several wetland species. Whereas the study species displayed a wide range of responses, intense soil reduction below -200 mV adversely affected growth and biomass accumulation in the majority of these species. It is clear that high oxygen demand in soil resulting from intense reduction influences oxygen transport and release to the rhizosphere. In addition, root elongation and shoot growth are profoundly influenced by the intensity and capacity of soil reduction.

INTRODUCTION

Numerous reviews and book chapters on plant responses to soil waterlogging are available that provide detailed literature synthesis on this topic (Armstrong and others 1994; Drew 1990, 1997; Hook and Crawford 1978; Jackson and others 1991; Kozlowski 1984a, 1984b, 1997; Pezeshki 1994; Vartapetian and Jackson 1997). Despite this wealth of literature, close examinations reveal that in most studies the status of soil oxidation-reduction conditions has not been reported. Although some researchers have reported oxygen concentrations in the root medium, such measure in wetland soil does not provide adequate information to allow evaluation of the intensity of soil reduction (DeLaune and Pezeshki 1991). This point is important because in wetland systems most plants are well adapted to endure soil-oxygen deficiency but may differ in ability to withstand certain levels of intense soil-reducing conditions.

In a typical flooded wetland soil, plants respond to the soil physicochemical changes. These responses may lead to a wide range of plant-stress symptoms.

Although various plant responses to flooded soil conditions have been addressed in numerous publications, little information can be found on the relationship between wetland plant functions and the two aspects of soil redox potential—the intensity and the capacity of reduction. The reduction of the inorganic redox systems in a flooded soil may be characterized in intensity or capacity terms. The intensity factor determines the relative ease of reduction whereas the capacity factor refers to the amount of the redox system undergoing reduction (DeLaune and Pezeshki 1991). From a plant physiological-ecology standpoint, there are many uses of interpretations of redox processes in soils; one example is that the knowledge of the soil redox potential represents an indication of the oxidation-reduction status of

various soil compounds. For example, a redox potential of zero mV indicates that oxygen and nitrate are not likely to be present and that the bioreducible iron and manganese compounds are in a reduced state. At this same potential, however, sulfate is stable in the soil with no sulfide being formed, which is toxic to plants. A redox potential of +400 mV indicates that oxygen may be present even though there may be excess water in the soil (DeLaune and Pezeshki 1991). Thus, the primary objective of the present paper is to summarize and assess evidences on the significance of the intensity and capacity of reduction in soils to wetland plant functioning. We will emphasize the relationships between soil flooding, reduced soil conditions (low soil redox potential, Eh), the components of the soil oxidation-reduction system, namely the intensity and the capacity of reduction, and their influence on internal oxygen transport, rhizosphere oxygenation, root and shoot growth, and survival of wetland species.

Soil Oxidation-Reduction Potential (Eh)

Soil flooding initiates a chain of reactions leading to reduced soil conditions (low soil redox potential, Eh). These reactions include physical, chemical, and biological processes that have significant implications for wetland plant functioning, survival, and productivity (see Gambrell and others 1991, Gambrell and Patrick 1978, Ponnampetuma 1984). Physical processes include restriction of soil-atmospheric gas exchange and depletion of soil oxygen needed for root respiration. Once flooded, the limited supply of oxygen in floodwater is depleted by roots, soil microorganisms, and soil reductants rapidly (Ponnampetuma 1972). The depletion of oxygen results in a series of chemical changes in soil including accumulation of CO₂, methane, N₂, and H₂ (Ponnampetuma 1984). The processes that follow include denitrification, reduction of iron, manganese and sulfate, and

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changing soil pH and Eh (Gambrell and others 1991). In a typical series of reduction, NO_3^- is reduced to NO_2^- , followed by reductions of Mn^{+4} to Mn^{+2} , Fe^{+3} to Fe^{+2} , SO_4^{2-} to S^{2-} and accumulations of acetic and butyric acids produced by microbial metabolism (Gambrell and Patrick 1978, Ponnamperna 1984). Thus, soil redox potential decreases (become more negative) in response to flooding (Gambrell and Patrick 1978; Patrick and DeLaune 1972, 1977; Ponnamperna 1984). Aerated soils have characteristic redox potentials in the range of +400 to +700 mV, whereas waterlogged soils may exhibit redox potentials as low as -300 mV.

In wetland soils, plants are faced with not only the lack of oxygen but also a substantial demand for oxygen in root medium (DeLaune and others 1990, van Wijk and others 1992). Such conditions create the potential for root oxygen loss to soil; thus, additional root stress (Brix and Sorrell 1996, DeLaune and others 1990).

Quantifying Soil Redox Conditions

Many of the terms used in the literature to define flooded soil conditions are difficult to quantify. For example, "flooded", "saturated", or "waterlogged" are frequently used to describe low oxygen supply conditions in soils. However, these terms hardly define root-zone conditions (DeLaune and Pezeshki 1991). In addition, due to the absence of oxygen in most "waterlogged" soils, methods used for the measurement of oxygen content and oxygen diffusion rate in well-drained soils cannot be used effectively (Gambrell and others 1991).

In contrast to the mostly nonquantifiable terms mentioned above, soil Eh is a useful term because it can be measured easily in the laboratory and in the field. The electrodes are relatively easy to build and handle under most conditions (for details see Faulkner and others 1989; Patrick and DeLaune 1972, 1977). Furthermore, quantifying soil Eh is particularly advantageous in periodically flooded soils because the range of Eh is much wider, ranging between approximately -300 to +700 mV, than either aerated or permanently waterlogged soils (DeLaune and Pezeshki 1991). Thus, soil Eh measurement is perhaps the best available quantifying tool of defining soil chemical status in wetland systems (Patrick and DeLaune 1977).

Intensity and Capacity of Reduction

The reduction of the inorganic redox systems including oxygen in hydric soils following flooding can be described in "intensity" and "capacity" terms. The intensity factor determines the relative ease of the reduction, whereas the capacity factor denotes the amount of the redox system undergoing reduction, e.g., oxygen consumption at root interface. It is represented by the free energy of the reduction, or, more commonly, by the equivalent electromotive force (EMF) of the reactions (Patrick and others 1986). In natural systems such as soils where there is biological activity and where many redox systems function, the oxidation-reduction or redox potential is ordinarily used to denote the intensity of reduction. The capacity factor of a redox system probably can be best described in terms of its oxygen equivalent (Kludze and DeLaune 1995, Reddy and others 1980). The capacity factor of the various redox systems can vary from one soil to another.

Proper evaluation of wetland plant responses to soil flooding requires evaluation of both intensity and capacity of soil reduction because these two components influence oxygen demand (Kludze and DeLaune 1995). DeLaune and others (1990) were the first to demonstrate that oxygen demand (capacity of reduction) in conjunction with intensity of reduction (as determined from soil Eh measurements) in the root medium was important to predicting wetland plant functioning. Furthermore, they noted that using oxygen-depleted solutions by nitrogen gas introduction did not represent a high root-oxygen demand environment; thus, they were a poor analogue of wetland soils. DeLaune and others (1990), Kludze and others (1993), and Sorrell and others (1993), using titanium citrate solution to create a high oxygen-demand root environment, reported that root oxygen transport and release were affected by such conditions in several wetland species. However, such a solution, while a significant improvement over de-oxygenated solution, at best mimics wet soil conditions (Kludze and DeLaune 1995); but, it does not represent other important characteristics of wet soils including the soil's capacity for phytotoxin production that has a significant effect on most wetland species. There is a critical need for development of reliable methods for quantifying capacity of reduction in soils to complement the more easily measured reduction intensity (Eh).

Plant Responses to Reducing Soil Conditions: The Internal Oxygen Transport System

In wetland plants, usually an extensive oxygen transport system of aerenchyma tissue facilitates oxygen diffusion from aerial parts to the roots. Such a system may exist in roots, stems, and leaves but is found primarily in roots (Armstrong and others 1994). This system allows a plant to transport the needed oxygen to the roots for maintaining aerobic respiration and to oxidize reducing compounds in the rhizosphere. In addition, the internal system of large gas spaces also reduces internal volume of respiring tissues and oxygen consumption, thus, enhancing the potential for oxygen reaching the distant underground portions of the plant (Armstrong and others 1994, 1996). Due to such advantages, the oxygen transport system has been considered as a major mechanism critical to a plant's ability to cope with soil anaerobiosis (Armstrong and others 1991, 1994, 1996; Drew 1990, 1992, 1997; Hook and Crawford 1978; Kozłowski 1982, 1984a, 1984b, 1997; Pezeshki 1994, Teal and Kanwisher 1966).

Root oxygenation helps plants overcome intense anaerobiosis (Armstrong and others 1994, 1996) and has important ecological implications in wetlands. For instance, the vigor and productivity of *Spartina alterniflora* were found to be positively correlated with substrate redox potentials because of the interaction with root aeration (DeLaune and others 1983). Two related factors contribute to limit plant growth under highly reduced soil conditions. First, the low Eh levels represent an oxygen-deficient system. Second, soil phytotoxins, the byproducts of low soil Eh, may continue to accumulate to concentrations that the roots' oxidizing power can no longer adequately ameliorate them (Mendelssohn and others 1981, Ponnamperna 1984, Teal and Kanwisher 1966). Under such conditions, the roots must rely more heavily on anaerobic respiration or transport sufficient

oxygen to roots to maintain aerobic respiration, lessening its capacity to oxidize the rhizosphere.

Internal plant air space results from aerenchyma tissue formation that is enhanced in many wetland species in response to flooding and is critical to wetland plant functioning in flooded soils (Drew and others 1985, Kozlowski 1997, Schat 1984). The effectiveness of the gas transport is primarily dependent on two factors: first, the resistance to diffusion that is proportional to root length and inversely proportional to root porosity; second, the oxygen demand along the diffusion path resulting from respiratory needs as well as oxygen leakage from the roots into the rhizosphere (Armstrong 1979, Luxmoore and others 1972). It is known that oxygen demands of roots and rhizosphere are competitive because, in flooded soils, these systems compete for the plant pool of oxygen simultaneously (Armstrong and Beckett 1987; Armstrong and others 1991, 1994). As soil reduction continues, there is a progressively greater demand imposed upon roots for oxygen (DeLaune and others 1990).

Soil Oxidation-Reduction, Plant Oxygen Transport, Functioning, and Growth

There is a limited body of data on the relationship between functional aspects of gas transport within plants and soil oxidation-reduction conditions. In a few studies that evaluated the relationship between plant responses and the intensity of soil reduction, it became evident that intense soil reduction (low soil Eh) promoted oxygen loss from root to the rhizosphere (fig. 1). For instance, in some wetland species, high correlation ($r = 0.96$) was found between radial oxygen loss (ROL) from roots and soil Eh intensity; i.e., there was an increasingly higher oxygen loss rate as soil Eh became more reduced (Kludze and DeLaune 1995). In addition, low soil Eh led to decreased leaf carbon assimilation (fig. 2) and substantial inhibition of root elongation (fig. 3).

In *S. patens*, a dominant U.S. gulf coastal marsh species, root porosity increased as soil Eh decreased, resulting in root porosity of 22 percent in plants grown at +200 mV whereas porosity was 45 percent in plants grown at -300 mV. Also, ROL was significantly greater for plants in -300 mV Eh treatment as compared to +200 mV Eh (Kludze and DeLaune 1994). Other studies have shown similar responses for root porosity-soil Eh intensity relationship in other wetland plants including swamp and bottomland woody species (Kludze and others 1994, Pezeshki and Anderson 1997). In contrast, Brix and Sorrell (1996) reported that root porosity in two wetland species, *Phalaris arundinacea* and *Glyceria maxima*, did not change in response to reducing Eh in root medium to as low as -250 mV. However, their experiment lasted only 12 days, of which the Eh in the root medium was at -250 mV for the last 7 days; thus, plants may not have had adequate time for response. Alternatively, the two species may have already had full-scale porosity development prior to treatment initiation. However, this is an unlikely scenario because porosity ranged from 5.3 to 11.6 percent, well below the range reported for many wetland plants. The range of porosity in many wetland species is much higher, particularly if grown under low soil Eh conditions (Kludze and DeLaune

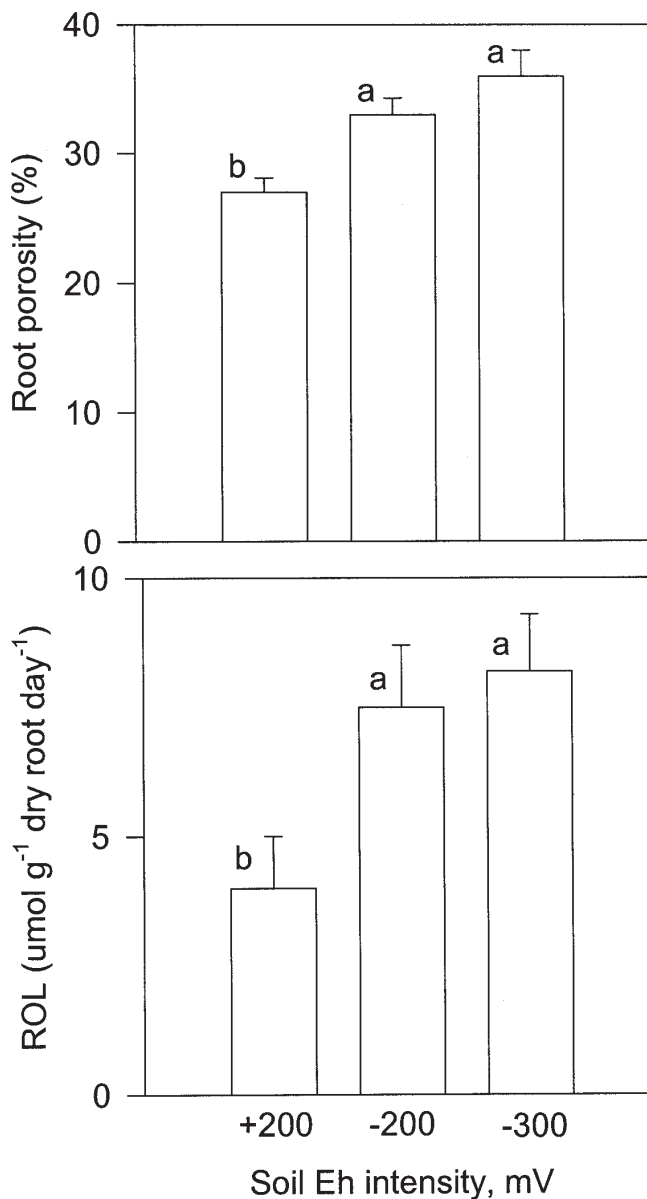


Figure 1—Root porosity (POR) and radial oxygen loss (ROL) in *Spartina patens* grown under various soil redox intensity for 50 days. Bars represent SE. (Redrawn from Kludze 1994.)

1994, Kludze and others 1994). In a study conducted on *Taxodium distichum*, significant increase in root porosity and ROL was noted at Eh intensity of -240 to -260 mV in root medium (Kludze and others 1994). ROL increased from 12.7 in control to 42.3 mmol O₂ per gram per day. Similarly, root air space increased from 13.3 to 41.4 percent in response to the intensity of reduction. In *Oryza sativa* (rice), ROL increased in response to a drop in soil Eh concomitant with root porosity that increased from 26.8 to 35 percent when Eh dropped from +200 to -300 mV (Kludze and others 1993).

Despite the reported increase in aerenchyma tissue formation in many wetland species and, thus, the increase in porosity in response to reducing soil conditions, such increase may not be sufficient to satisfy the root respiratory need for oxygen, perhaps due to the greater ROL in response to high intensity of reduction. Pezeshki and others

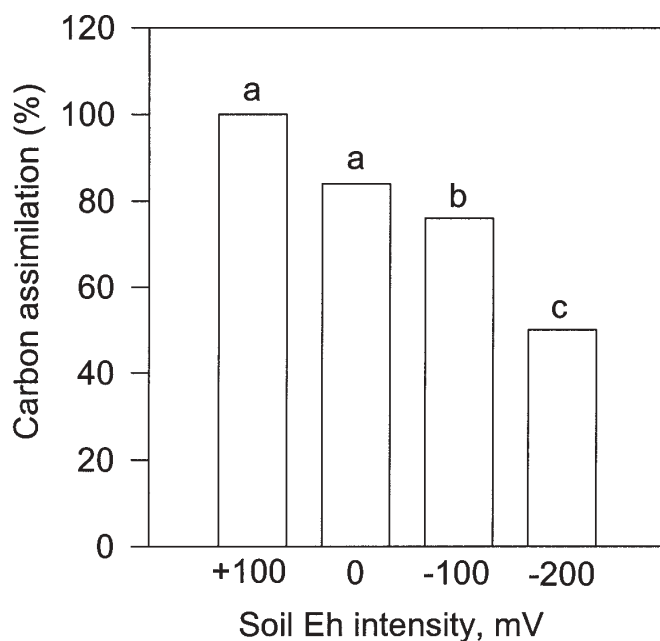


Figure 2—Carbon assimilation in *Spartina patens* grown under various soil reduction intensities. Data were collected at 17 days after growth in incubated soils. Values followed by the same letter are not significantly different at the 0.05 level. (Redrawn from Kludze 1994.)

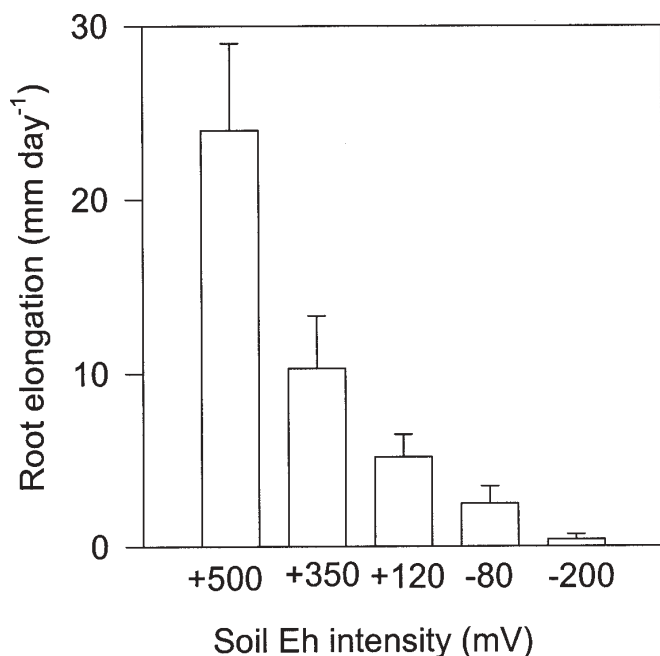


Figure 3—Root elongation in *Spartina patens* grown under various soil reduction intensities (Eh, mV). Data were collected on plants grown in different rhizotrons in which soil Eh was manipulated using various air/nitrogen gas mixtures. (Redrawn from Pezeshki and DeLaune 1990.)

(1991, 1993) concluded that despite a substantial enhancement of aerenchyma tissue formation in *Spartina patens*, alcohol dehydrogenase activity continued to be higher in flooded than control plants indicating continued oxygen stress in the roots of flooded plants. In addition, the increase in ROL reported under intense soil Eh may explain the reported reductions in root growth of several wetland species under low soil Eh conditions. For instance, in *Spartina patens* root and shoot dry weights decreased by 40 percent and 25 percent as soil Eh dropped from +200 mV to -300 mV, respectively. Results clearly indicated the influence of soil Eh intensity on growth of this marsh species. It also was demonstrated that roots were more sensitive to Eh intensity than shoots (Kludze and DeLaune 1994). Pezeshki and DeLaune (1990) reported cessation of root growth in *S. patens* at soil Eh below -100 mV (fig. 3). In addition, Pezeshki and others (1991) noted smaller root systems in *S. patens* under reducing conditions and concluded that such reduction in sink size may, in part, be responsible for a negative feed-back inhibition of photosynthesis resulting in a reduction in productivity of this species. DeLaune and others (1990) studied plant responses to the intensity of soil reduction using a titanium-citrate solution. They demonstrated that the intensity of the reduction in growth medium and the resulting demand for oxygen in the root zone exerted significant influence on plant physiological functioning.

The redox capacity factor is also important although much less is known about its effects on wetland plants than is known about the effects of the intensity factor. In fact, two different soils with the same level of intensity of reduction may differ substantially in the capacity for reduction. Soil reduction capacity can be determined using measurements of soil respiration CO₂ and calculating oxygen equivalent by stoichiometry (Kludze and DeLaune 1995). Levels of soil redox capacity may be created or manipulated, or both, by providing extra carbon and energy source (organic matter) to the soil while maintaining the same redox intensity level. In an experimental set-up, reduction capacity may be controlled by adding different amounts of granular D-glucose to the root medium, which is also maintained under preset reducing conditions (Eh < +350 mV) (Kludze 1994).

As was the case for the intensity of Eh reduction, differences in Eh capacity among wetland soils may influence many plant functions (figs. 4, 5) including oxygen transport, rhizosphere oxygenation, photosynthetic rates, and, thus, many aspects of plant functioning (Kludze and DeLaune 1995). Studies showed that increased Eh capacity under a constant Eh intensity of -200 mV did not have any significant effect on root porosity in *S. patens*, but oxygen release was increased in response to the increasing Eh capacity (Kludze and DeLaune 1995). However, the authors reported that there was a threshold of Eh capacity beyond which oxygen release remained constant or decreased, or both, in this species. The response was attributed to the potential effects of several factors such as soil phytotoxins as well as plant physiological responses including stomatal closure. However, the reasons for such a response remain unknown. Plant carbon fixation, root, and shoot growth were significantly inhibited in *S. patens* under increasing soil-reduction capacity. Root and shoot dry weights decreased

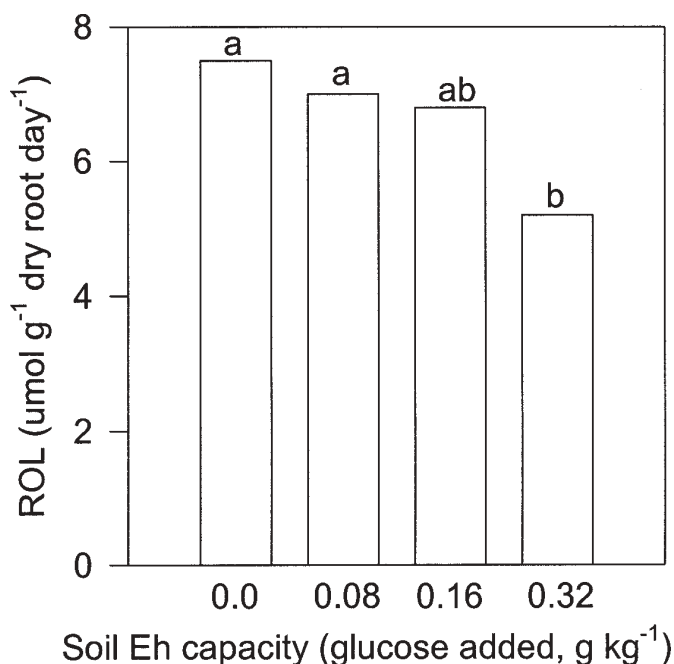


Figure 4—Radial oxygen loss (ROL) in *Spartina patens* grown under various soil reduction capacities while the reduction intensity was maintained at -200 mV. Values followed by the same letter are not significantly different at the 0.05 level. (Redrawn from Kludze and DeLaune 1995.)

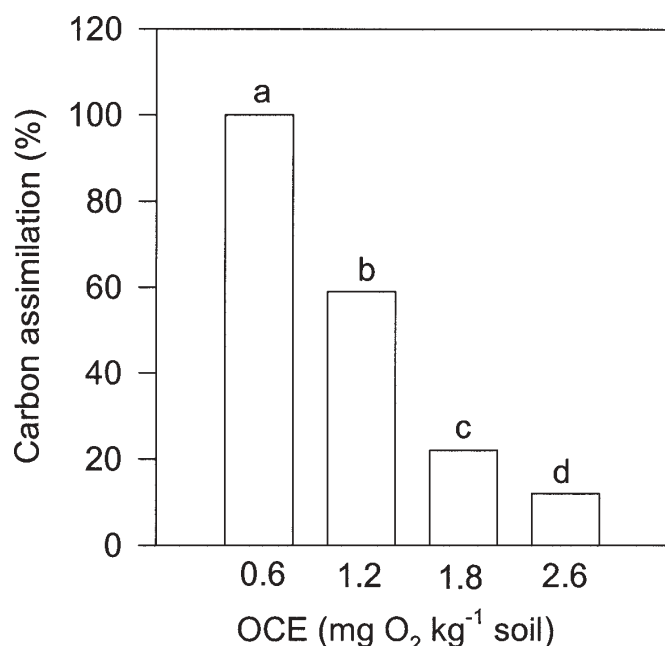


Figure 5—Carbon assimilation in *Spartina patens* grown under various soil reduction capacities. The soil redox intensity was maintained at -200 mV across all treatments. Data were collected at 17 days after growth in incubated soils. Values followed by the same letter are not significantly different at the 0.05 level. OCE: Oxygen Consumption Equivalent, mg O₂ per kilogram soil. (Redrawn from Kludze and DeLaune 1995.)

by 70 and 37 percent in high reduction capacity conditions compared to control plants, respectively (Kludze and DeLaune 1995).

In addition to the effects on growth, limited data suggest that both the intensity and capacity of reduction may govern nutrient uptake in wetland plants. In a study of seedlings of two bottomland woody species grown in soil suspension maintained at three Eh levels, $+560$, $+340$, and $+175$ mV, fertilizer ¹⁵N uptake decreased with decreasing soil redox potential, a response to the intensity of reduction (DeLaune and others 1998). Phosphorus uptake by *Typha domingensis* was inhibited in response to decreases in soil redox potential (intensity of reduction) in rooting medium. Increasing capacity of reduction (using a titanium citrate solution) resulted in a further decrease in phosphorus uptake (DeLaune and others 1999), further confirming the effects of reduction capacity on nutrient uptake.

CONCLUDING REMARKS

Based on the limited data discussed above, both intensity and capacity of reduction appear to influence plant functioning in wetland ecosystems. In wetland soils, plants are faced with a substantial demand for oxygen in the rhizosphere and the potential for loss of oxygen to the soil resulting in additional root stress. As soil reduction continues and intensifies, there is a progressively greater demand imposed upon roots for oxygen, and, thus, a greater potential for loss of oxygen to the rhizosphere. The severity of oxygen loss and the effects of reduction intensity and capacity on plant functioning appear to be broad across wetland species. The need for additional data on various aspects of plant functioning and growth in wetland ecosystems in response to soil redox conditions, especially capacity of reduction, is clear. Redox potential measurements collected in soils using platinum electrodes provide information only on intensity of reduction. In studying plant response to a reducing environment, methods must be developed to evaluate the influence of capacity of soil reduction in addition to the intensity of soil reduction on wetland plant growth and functioning.

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